PYROLA APHYLLA: A MORPHOLOGICAL STUDY.

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(WITH PLATE XVII)

IT would seem very strange if there really existed a truly leafless species in a genus like Pyrola, of which all the other representatives are not only leafy, but even evergreen. One might think at a first glance that the lack of proper leaves would influence the species so much in its mode of growth, as a saprophyte or parasite, as to warrant its segregation from the genus Pyrola. Entire genera devoid of proper leaves are not so very scarce in the phanerogams, but in no case does there exist a genus which contains autophytic, saprophytic, and parasitic species. There are several families, on the other hand, in which we meet with both leafy and leafless genera; for instance, the apparently leafless Epirhizanthes among the Polygalaceæ; Voyria and Voyriella among the Gentianaceæ; Monotropa, Sarcodes, Pterospora, etc., among the Pyrolaceæ; Neottia, Corallorhiza, etc., among the Orchidaceæ; and, finally, Baillon's remarkable Geosiris among the Iridaceæ.[1] These instances are familiar to us, but we are unable to cite any genus which has both autophytic and parasitic species, with the exception, as it has been believed, of Pyrola. The fact is, however, that, notwithstanding statements made by such prominent authors as DeCandolle and Hooker, the plant is not by any means aphyllous, but has evidently received its name for the same reason that Galax was named *aphylla* by Linnæus, the original specimens having but imperfectly represented the species. Thus has DeCandolle described our Pyrola as "foliis veris nullis" and as a "species absentia foliorum spectabilis et quasi ad Monotropeas vergens;" while Hooker goes still further in stating "folia omnino nulla."

[1] For references consult the bibliography appended to this article.

The figure in Hooker's work shows distinctly that his specimen was but fragmentary. Nuttall, shortly after Hooker, corrected this mistake by stating "occasionally it produces, near the root and on infertile shoots, a few small, ovate, or lanceolate greenish leaves." It is very surprising that Gray in later years should still have described it as "leafless, doubtless parasitic," and as "a peculiarly interesting plant on account of its living the parasitic life of the Monotropeæ." To Nuttall, therefore, belongs the credit of having discovered the leaves of this singular plant which Smith at first described as destitute of leaves, and accordingly named it "leafless wintergreen." These contradictory statements, however, have led the writer to investigate the matter fully, after having secured some excellent living specimens from Amador county, California, which were kindly collected by Mr. Geo. Hansen. Besides confirming Nuttall's observations of the presence of proper leaves, I have detected a few peculiarities which will be presented in this paper.

The accompanying *fig. 1* represents a mature and very carefully collected specimen of our plant, and we notice here several underground shoots, of which one bears a rosette of leaves at its apex (*L*), in the same manner as in other species of Pyrola. In considering the leaves by themselves, they are, as described by Nuttall, rather small, but provided with a distinct petiole and a blade, varying from lanceolate to broadly ovate, obtuse, or slightly pointed (*figs. 2, 3*). These leaves were green, and the chlorophyll became still more conspicuous by immersing the leaves in strong alcohol, which readily assumed a deep green color, which afterwards turned dark brown from the large content of tannin in the cell sap. As regards the minute structure of these leaves, we did not observe any peculiarity by which our species might be separated from the other species of Pyrola, and there is absolutely no character whatever that might warrant the supposition that our plant lives a saprophytic or a parasitic life. The epidermis is perfectly normal and covered by a thick and wrinkled cuticle, common to evergreen leaves; stomata are present on both faces of the blade, but are most numer-

ous on the lower surface; no hairs or glands were observed on either face. The chlorophyll-bearing tissue is differentiated into a palisade tissue of about two layers on the ventral face of the blade, and an ordinary pneumatic tissue, the cells of which are roundish and loosely connected with each other, leaving intercellular spaces of quite considerable width. The mestome bundles possess all the elements as found in other dicotyledons, and are supported by a collenchymatic tissue which makes the nerves very prominent on the lower surface of the leaf.

Besides these completely developed leaves, our plant possesses also scale-like ones, which are much more numerous, covering not only the underground shoots, but also the base of the inflorescences (i^1 and i^2 in *fig.* 1). Very characteristic of *Pyrola aphylla* is the profuse development of axillary buds, which are readily observed upon the underground stems and at the base of the aerial floral and vegetative shoots. These axillary buds, however, are restricted to the scale-like leaves, since I failed to detect any such in the axils of those provided with petiole and blade. The first two leaves of such axillary buds are situated to the right and left of the diminutive bud axis, while the third and fourth appear almost in regular alternation with these, those following, on the contrary, forming an ordinary spiral.

Upon examining the stem underground we notice in our figure (*fig.* 1) two long branches (b^1 and b^2) with elongated internodes, which show an ascending curvature from the roots, from which point they creep horizontally underneath the surface of the soil, until they finally push up through it, either terminated at once by the inflorescence or first by a rosette of proper leaves. It is easily understood that it has been the collecting of just such underground branches, terminated by inflorescences and not preceded by a rosette of leaves, which has misled botanists to consider our plant as aphyllous and parasitic. The anatomical structure of these underground branches, which constitute the rhizome of *Pyrola aphylla*, is, however, that of a true autophyte,

showing the well-known elements of normally developed tissues. There is a wrinkled cuticle covering the thick-walled epidermis, inside of which follows a heavy layer of cork parenchyma of rather closely packed polyhedric cells, which border on a thin-walled endodermis. This endodermis encircles the leptome and hadrome, the last of which has distinctly lignified cell walls, while an ordinary pith occupies the innermost part of the central cylinder. Tannin was observed in abundance in the cells of the bark and epidermis.

In comparing the structure with that of the aerial flower-bearing stem, we notice only a few divergencies. The bark contains chlorophyll, and a closed ring of stereome is developed around the central cylinder, of which the pith occupies the larger part. In combining these anatomical features of the leaves, the aerial and subterranean stem, there is so far no indication of our plant being a parasite or saprophyte or in any other way differing from the other species of Pyrola.

The last organ of the plant, which is not to be overlooked, is the root, the main and the adventitious. Only a part of the main root was preserved in our specimens (*R* in *fig.* 1), and it is by no means certain whether this dark colored and slightly branched root is the main root or merely a branch. It is from this root, however, that the subterranean shoots have developed as true root-shoots, a fact that is readily observed in *fig.* 1. We not only observe that the two long underground branches proceed directly from this root, but also the development of two dense clusters of shoots with more or less curved apices, all of which are beginning to develop into underground creeping stems, like the two larger ones described above (b^1 and b^2). Our plant shows then a strongly pronounced vegetative propagation, which perhaps has reached a higher development in this than in any other species of Pyrola. Adventitious roots were also observed. They are rather thin and show only a few ramifications. Their position is somewhat peculiar, since they break out a short distance above the scale-like leaves, and either to the right or left of the axillary buds.

Besides the fact that we have not been able to detect any haustoria upon the roots, the interior structure is sufficient to show the nature of our plant, whether it is an autophyte, a parasite, or a saprophyte. The presence of green leaves, however, is sufficient to determine the question whether the plant is a saprophyte, and a general consideration of the anatomy of the roots will suffice to convince any observer that *Pyrola aphylla* is no parasite either. Root-hairs are developed from the epidermis, inside of which there is a hypoderm of rather large cells, which surrounds a bark-parenchyma of normal structure and packed with starch, but without any trace of fungal mycelia. The endodermis is perfectly normal and surrounds, together with the pericambium, the five groups of leptome, alternating with a corresponding number of hadrome groups, while the innermost part of the central cylinder is occupied by a few strata of conjunctive tissue.

Pyrola aphylla shows, therefore, a striking ability to propagate by means of axillary buds developed upon the underground stems, and likewise by adventitious buds which push out very freely from the roots. Propagation by seeds is not excluded, and each capsule contains a large number of very minute, but mature seeds. By bringing these facts together with the anatomical structure of the vegetative organs, it may be seen that our plant shows no sign of living a parasitic life or even a saprophytic one, but that it is a true autophyte. This becomes the more evident when we compare our species with its nearest relatives, of the genus Pyrola itself, of Moneses and Chimaphila.

From the writings of Irmisch we have learned that a similar reproduction by root-shoots takes place in *Pyrola secunda*, *P. chlorantha*, and in *Moneses uniflora*. Besides, we have succeeded in finding similar shoots from the roots of *Pyrola picta*, *Chimaphila umbellata*, and *C. maculata*. The morphological characters of the vegetative organs of the species of Pyrola depend especially upon the development of the proper leaves, whether they precede or are contemporary with the flowers. According to Irmisch, some of the leaves develop in the same year as

the flowers in *Pyrola minor*, while in *P. secunda* and *P. rotundifolia* all the proper leaves have appeared during the year previous to the flowering. It is to be noted that a few rudimentary scale-like leaves occur also in these species, preceding and succeeding the proper ones. While the inflorescence is strictly terminal in the above mentioned species of Pyrola, Irmisch observed also lateral ones in *P. chlorantha*, and it is interesting to notice that these lateral inflorescences possessed only undeveloped leaves at their bases.

In our plant, *Pyrola aphylla*, we have both terminal and lateral inflorescences, the terminal being, perhaps, constantly preceded by normal leaves (*L* in *fig. 1*), which appeared during the year previous to the flowering, agreeing in this respect with *P. secunda*, *P. chlorantha*, and *P. rotundifolia*. No axillary buds were observed in the axils of the green leaves, a fact that furnishes another illustration of the great resemblance which exists in the vegetative organs of Pyrola. The most conspicuous character of *P. aphylla*, if we merely compare the vegetative organs, lies in the scanty foliage of proper leaves, which, however, has become in part replaced by an unusually large number of scale-like ones.

If we compare our plant with Chimaphila, of which we have examined *C. umbellata* and *C. maculata*, we shall find many analogies. We have already stated that we observed root-shoots in both of these species, and *fig. 4* shows the base of an old plant of *C. maculata*, with a young shoot pushing out from one of the lateral roots (*R. S.*). The species of Chimaphila also develop long horizontally creeping and branching rhizomes, which in a specimen of *C. umbellata* reached a length of two-thirds of a meter. The aerial shoots of Chimaphila differ, however, from those of *Pyrola aphylla* and the other species mentioned above, in that the proper leaves support buds, which develop during the following year.

In respect to the absence of scale-like leaves at the base of the inflorescence and above the proper leaves, Chimaphila agrees with several of the species of Pyrola, but not with *P. minor* and

P. aphylla. It seems, on the whole, that these members of the Pyrolaceæ, Pyrola, Moneses, and Chimaphila, form a very natural group by themselves, if we consider their morphological characters, and their floral and vegetative structures. While *Pyrola secunda*, *P. aphylla*, *P. picta*, and *P. chlorantha* are the only species which have been observed to produce root-shoots, we should not feel surprised if this be the case also with all the other species, as in Moneses and Chimaphila. But we doubt very much whether any of these genera live as true saprophytes, although the supposed related Monotropeæ are known to live as such.

There is yet another point of interest in the life history of the Pyrolaceæ which we should like to touch upon, even though it may seem somewhat foreign to the main subject of this paper. The germination of the Pyrolaceæ is almost unknown, and with the exception of *Pyrola secunda* and Monotropa, none have been examined at this early stage of development. In his description of the germination of *P. secunda*, Irmisch points out the lack of two opposite cotyledons, while a series of about ten scale-like leaves, all underground, precede the proper ones. These rudimentary leaves were pale, and they were situated at some distance from each other upon the underground part of the stem. Buds were observed in the axils of these leaves, and some of them had already pushed out so as to form ascending shoots. Secondary roots were seen in several cases to break out above a number of these buds. This manner of germinating, with no proper cotyledons, is rather rare among the dicotyledons, but is especially characteristic of the parasitic forms, Orobancheæ (excepting Lathræa), Balanophoreæ, Cuscuta, etc., besides the saprophytic genus Monotropa. It seems very strange that *Pyrola secunda* should exhibit a similar manner of germination, since it does not otherwise behave as a saprophyte. It is the more surprising, also, in view of the fact that *Chimaphila maculata* germinates in the same way as the majority of the other dicotyledons. We succeeded in finding a number of seedlings of this species in the month of July, while we were digging out some

mature specimens for the purpose of examining the rhizomes. These seedlings, one of which is figured (*fig. 5*), showed then a long hypocotyl (*H* in the figure), two normal green cotyledons (*Cot.*) which were almost sessile, the blade oblong or approximately obovate. The first two leaves, succeeding the cotyledons, had a distinct petiole and an oblong blade, while the third showed the first traces of dentation and represented a tridentate leaf. The main root (*R*) was long, slightly branched, and covered with root-hairs; one pair of secondary roots (*r*) were developed just above the main one, but in no other place were such secondary roots observed upon these minute seedlings. Although *Chimaphila umbellata* is not uncommon in the vicinity of Washington, we have not yet been able to detect its seedlings, but it is not likely that they differ from those of *C. maculata*, as the manner of growth of these species is exactly the same. The species of Pyrola and Moneses demonstrate, on the contrary, a somewhat different mode of growth, which perhaps may be visible at the earliest stages of their development during germination.

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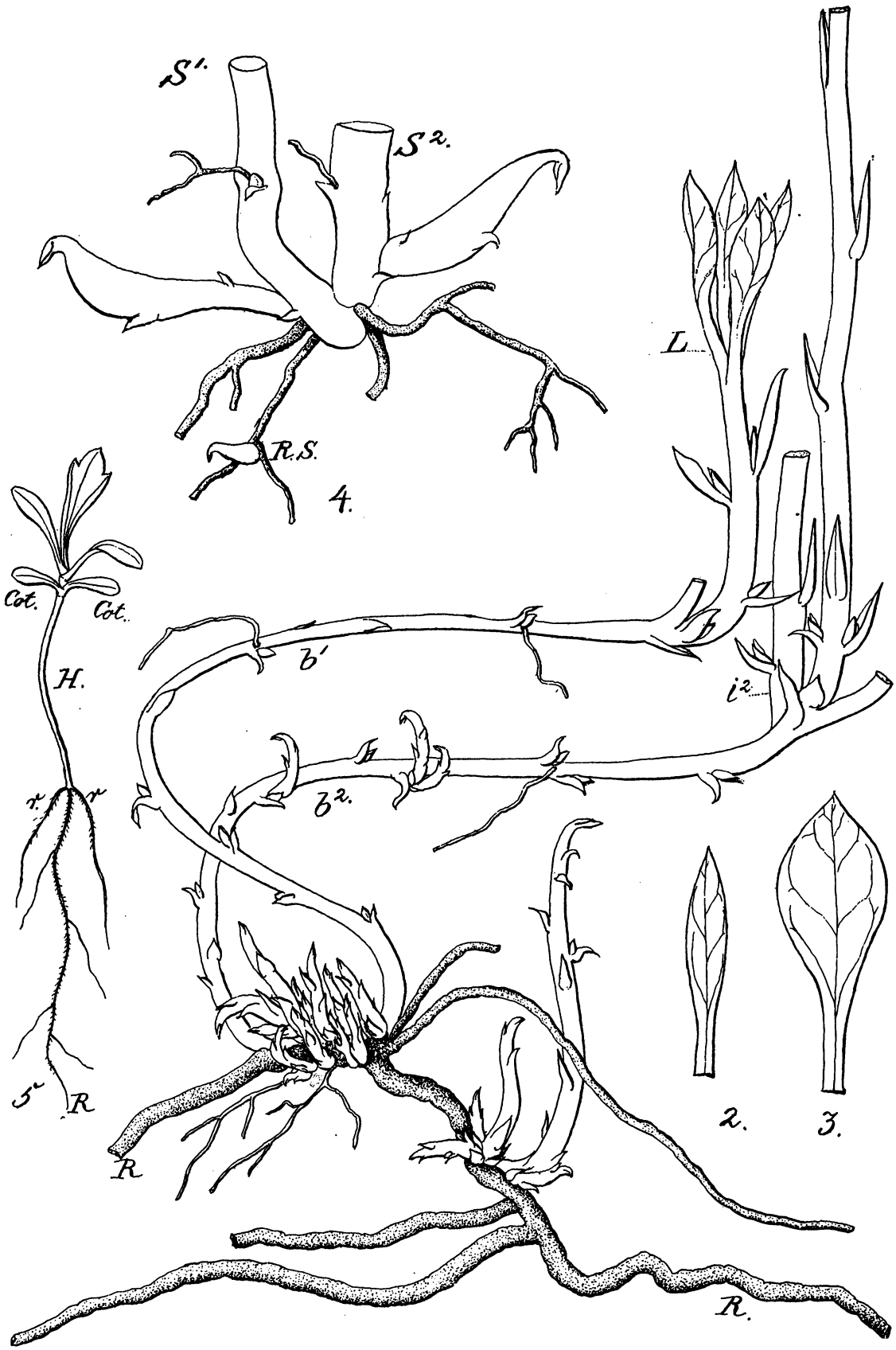
EXPLANATION OF PLATE XVII.

FIG. 1. A mature specimen of *Pyrola aphylla*. A rosette of proper leaves is to be seen at *L*; the base of two inflorescences at i^1 and i^2; b^1 and b^2 are the underground branches, which have developed from the root *R*, together with two clusters of small, ascending shoots. Natural size.

FIGS. 2 and 3. Leaves from the rosette. ×2.

FIG. 4. Rhizome of *Chimaphila maculata*, showing the base of two aerial stems (s^1 and s^2) with underground lateral shoots; a small root-shoot is to be seen at *R. S.* ×2.

FIG. 5. Seedling of *Chimaphila maculata*. *R* = the primary root; *r* and *r* = the first pair of secondary roots; *H* = the hypocotyl; *Cot.* = the cotyledons. ×3.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